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THE BIOLOGY OF *AGLAOPHAMUS NEOTENUS* (POLYCHAETA: NEPHTYIDAE), A NEW SPECIES FROM MAINE AND CANADA[1]

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The biology of the family Nephtyidae Grube, 1850, is poorly understood. Most of the literature deals with taxonomic aspects. Hartman (1950) provides a review of the morphological and taxonomic features of the family, and recognizes three genera, *Aglaophamus, Micronephthys,* and *Nephtys,* as does Pettibone (1963). Fauchald (1968 and 1977) adds a fourth genus, *Inermonephtys.* Hartman points out that due to many simliar structural characters the family has been considered a single genus by Cuvier (1817), Savigny (1820), Audonin and Milne-Edwards (1834), and Chamberlin (1919). Fauchald (1968) demonstrates that the genera *Nephtys* Cuvier, 1817, *Aglaophamus* Kinberg, 1866, and *Micronephthys* Friedrich, 1939, are separated by well-established morphological characteristics, especially the nature of the branchae or interramal cirri which may be involute, recurved, or absent as described by Hartman (1950). In recognizing the new genus *Inermonephtys,* Fauchald (1968) emphasizes the nature of interramal cirri, proboscidal papillation, and antennae to separate the four genera of Nephtyidae. Other diagnostic features used by Fauchald include aspects of the jaw, nuchal processes, acicular tip, and parapodial setation. General features of the genus *Aglaophamus* are given by Hartman (1950) and more recently by Fauchald (1968 and 1977) who recognizes 45 species.

The first description of nephtyid larvae was by Claparède and Metschnikow (1869). Since then brief descriptions of planktonic forms have been made by Fewekes (1883), Haecker (1896), Leschke (1903). Gravely (1908), McIntosh (1908), Fuchs (1911), D. P. Wilson (1936), Smidt (1944), Thorson (1946), and Rasmussen (1973). These forms have all been attributed to two or three species of *Nephtys.* No larval stages have been reported for *Aglaophamus* or *Micronephthys.* There are no recorded observations of nephtyid metamorphosis from the planktonic laravl stage to the benthic juvenile. There appears to be no record of a complete life history of any species of nephtyid from egg to adult. The annual gametogenic cycles for *Nephtys hombergii* and *N. caeca* are described by Olive (1978).

Information of the feeding habits of nephtyids is limited. Mileikovsky (1959) demonstrated the pelagic larvae of *Nephtys ciliata* are predatory on both bivalve and gastropod larvae. Blegvad (1914) stated that adult members of this family feed mainly on smaller worms, molluscs, and crustaceans. In two cases, Hunt (1925) found remains of spionid worms in *Nephtys hombergii.* Pettibone (1963) wrote that nephtyids are predatory in their feeding, as did Mare (1942), and Clark (1962). Mare found that worms seldom had gut contents when examined, but if material was present it consisted of the remains of other polychaetes. Day (1967)

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pointed out that nephtyids were generally thought to be carnivores, but doubts had arisen after studies of dense populations. Sanders (1958, 1960) considered *Nephtys incisa* a nonselective deposit feeder. Evidence from the present study shows *Aglaophamus neotenus* is a nonselective omnivore, feeding on sediment.

An undescribed species of *Aglaophamus* was first observed by the author in 1966 near the University of Maine's marine laboratory in Walpole, Maine. A dense population of animals was located off Wentworth Point in the Damariscotta River. The population extended from the intertidal zone to a depth of about 10 m. The sediment was a soft, silty mud. Adult animals were small (5 to 12 mm) and reproducing. Members of this species were later found at several other locations along the Maine coast including Montsweag Bay on the Sheepscot River, and the Orland River tributary to Penobscot Bay. Specimens were also sent to me by Dr. M. J. Dadswell of the Huntsman Marine Laboratory, which were collected from the St. John Estuary, Canada and tentatively identified as *Micronephthys* sp. They proved to be specimens of *Aglaophamus neotenus*, extending the range into Canada.

This paper describes the new species, its life history and biology.

Materials and Methods

Subtidal samples of adult specimens of *A. neotenus* were taken with an Ekman grab having an opening of 225 cm^2. Animals were separated by washing the sediment through a No. 60 stainless steel sieve (0.250 mm mesh). Juveniles were collected subtidally at Wentworth Point by skimming the upper 1 to 2 cm of bottom with a metal scoop. This sediment was washed through a No. 140 stainless steel sieve (0.105 mm mesh). Planktonic larval forms were obtained by towing a No. 20 plankton net (0.076 mm) along the edge of the dock at Wentworth Point or from a boat near other collecting sites. Salinity and temperature measurements were made using a Beckman portable induction salinometer.

Living material was kept in controlled temperature cabinets with temperatures approximating those of the water at the time of collection. Adults and sediments retained by sieves were placed in 2-liter Pyrex culture dishes. Some juveniles and plankton isolates of larave were kept in Boveri dishes. Others were placed in 100-ml Pyrex funnels which had stems removed and bases melted closed. A small amount of sediment was placed in the bottom of each funnel, then sea water, and larvae or juveniles were added. The funnel culture method facilitated observation of swimming or burrowing. Some adults were kept in an aquarium with sediment from Wentworth Point.

Larval stages raised in the laboratory were lecithotrophic and required no food. Feeding experiments with adults gave negative results and will be discussed below. After washing, all glassware was rinsed once with concentrated HCl and three times with distilled water. Sea water was collected from the dock at Wentworth Point and filtered through Millipore glass fiber prefilters (Type AP20) before use.

In artificial fertilization experiments, gravid males and females were teased open with fine forceps in separate 500-ml Pyrex fingerbowls containing filtered sea water. Eggs were washed through a 0.250 mm nylon mesh screen into clean fingerbowls and allowed to settle. The supernatant was decanted and fresh filtered sea water added. This was repeated until most detrital and coelomic material was removed. Ten drops of "sperm water" were added from a dish containing male worms. Dishes containing eggs were held at room temperature until cleavage was observed. Cultures were then kept at 10° C.

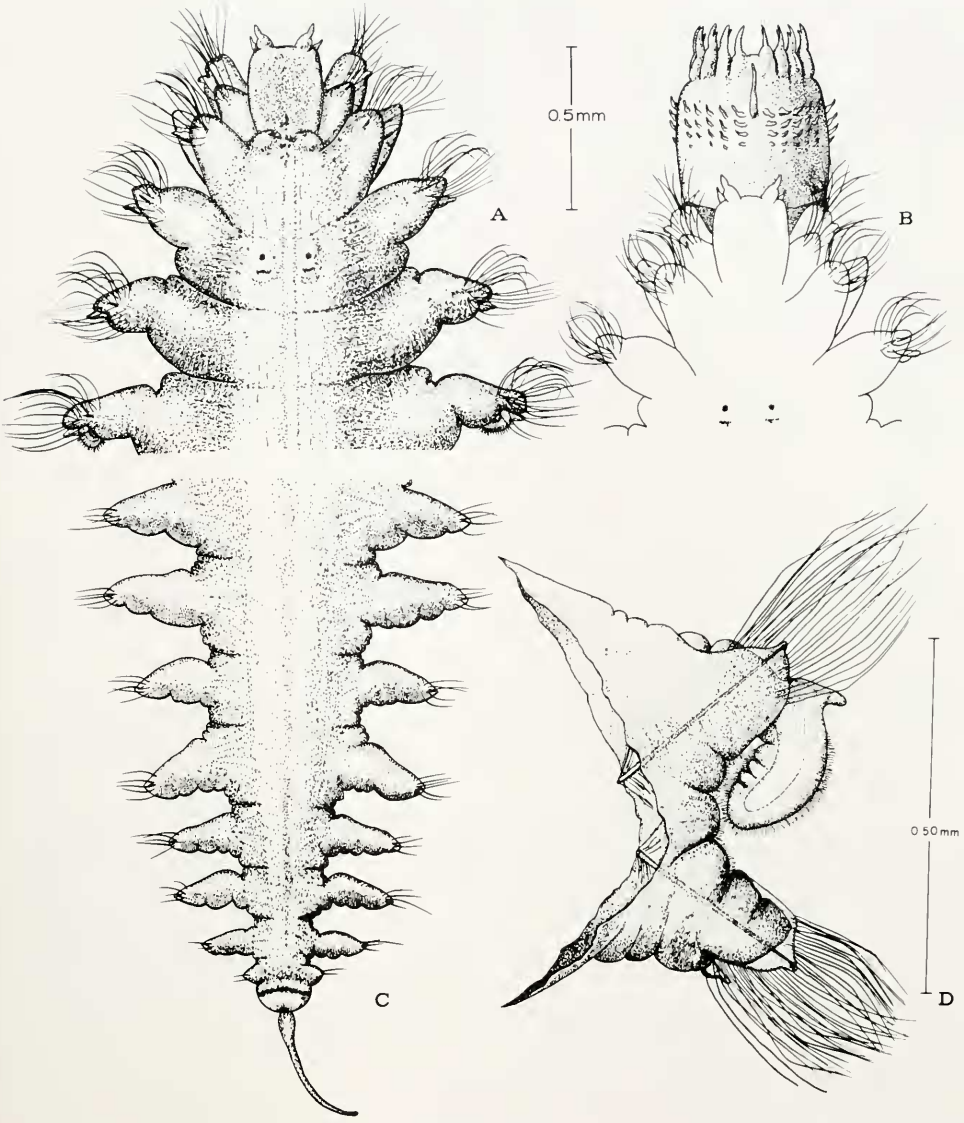

FIGURE 1. Adult specimen of *Aglaophamus neotenus*, new species: A, dorsal view of anterior end; B, view of anterior end with proboscis everted; C, dorsal view of posterior segments; D, anterior view of left, tenth, parapodial lobe.

Laboratory reared larval forms were cultured in 500-ml Erlenmeyer flasks at 10° C. Culture water was changed every second day by washing through a fine nylon mesh screen. Larvae retained on the screen were quickly and gently back-washed into fresh flasks with filtered sea water.

Hanging drop preparations were used to observe living gametes, cleaving eggs, larvae and juveniles. Glycerin mounts of preserved adults were studied to describe anatomical features. Living sperm were prepared as described by Franzen (1956), using Janus green B and neutral red vital stains.

Specimens were relaxed for study in a solution of propylene phenoxytol in sea water. A 0.15% solution was used for adults but was diluted approximately one-half for use with larvae. Worms were preserved in Kahles' solution and transferred to 70% ethyl alcohol for storage. Histological preparations included paraffin embedding, sectioning at 8 μ, and staining with hematoxylin and fast green.

Systematic Treatment and Results

Aglaophamus neotenus, new species

Type material

Holotype: National Museum of Natural History, Smithsonian Institution, USNM No. 47165, 1970, Gender female, 32 setigers, 10.3 mm long, 1.3 mm wide.

Paratypes (28): National Museum of Natural History, Smithsonian Institution, USNM No. 47166, 1970.

Material examined

The description is based on the holotype, paratypes, and specimens in the author's collection from Maine (Damariscotta River, Sheepscot River, and Orland River) and from Canada (specimens sent to the author by Dr. J. M. Dadswell, collected from the St. John Estuary).

Description

Adults very small, ranging from 5 to 12 mm long, 0.5 to 1.7 mm wide and having up to 32 segments.

Anterior end of body is blunt and narrow, body gradually widens in middle region, then narrows to the pygidium which carries an anal cirrus (Fig. 1C).

Prostomium rectangular, bears pair of anterodorsal antennae and pair of subterminal antennae (Fig. 1A). Antenna fleshy with bulbous base tapering to fine tip. Occasionally (in about 10% of worms examined) one or both ventrolateral antennae have a small lateral extension or bifid aspect. Nuchal organs arise dorsal, just posterior to prostomium, but are not always visible due to retraction, especially with preservation. Digitiform nuchal processes described by Fauchald (1968) for the genus *Ineromonephyts* are lacking.

Eyes visible dorsally on setiger three, dark red in color, subepidermal; each has a round, granular pigment spot, with a crescent of fine pigment granules posterior to it.

Parapodia small, biramous, with those on first and last setiger being reduced. Small, dorsal, notopodial cirri begin on setiger two, are replaced by branchae or interramal cirri from setiger five or six through 15 or 20, but occur again through last setiger. The neuropodial, post-setal lobe, produced ventrally on the parapodium, carries the ventral cirrus on all neuropodia. Ventral cirri are reduced posteriorly.

Branchae or interramal cirri slightly involute, heavily ciliated, and carry an accessory crirrus on the outer side of their nonbulbous base (Fig. 1D).

Each noto- and neuropodium bears an aciculum with fine, recurved tip (Fig. 2D); acicular lobes are pointed. Anterior setigers have smooth capillary, preacicular barred capillary, and postacicular spinous setae. Barred setae number

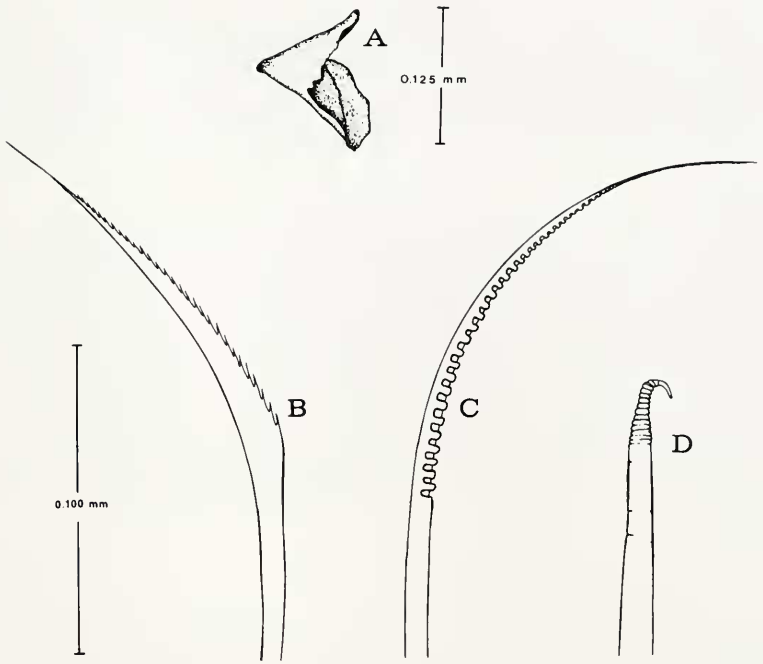

FIGURE 2. Adult specimen of *Aglaophamus neotenus*, new species: A, right jaw lying on its anterior surface, B. postacicular spinous setae, C, preacicular barred capillary setae; D, aciculum.

six to eight per fascicle and are replaced by smooth capillary setae at about setiger 20. Spinous setae are replaced by smooth capillaries over last few posterior setigers. Ornamentation of barred capillaries is on the outer one third of shaft (Fig. 2C). Spinous setae have blade-like edges subdistally, bearing fine spinets (Fig. 2B).

Pharyngeal region occupies setigers two through eight, is swollen due to retracted proboscis, and provides slightly upward-curving appearance to worm.

Proboscis cylindrical, with distal row of 16 or 18 papillae with 14 to 16 longitudinal rows of fine subterminal papillae behind distal papillae; five to six fine, pointed papillae occupy each subterminal row. A single, long, mid-dorsal subterminal papilla is present. Proximal surface of proboscis is free of ornamentation (Fig. 1B).

Jaws very small, about 125 μm on longest axis, color golden brown, base roughly triangular; an inner supportive ridge appears to be present, but jaw detail is difficult to determine due to small size (Fig. 2A).

Body coloration in living worms varies from creamy white to pink or light orange; females more pink or orange than males. Dorsally, prostomium is yellow; dark red, sometimes almost black pigment granules are scattered over its surface. A dark red pigment spot is located on the distal and slightly ventral end of the prostomium. Prostomial pigmentation can vary somewhat between individuals. Paired, dark red, pigment spots, located dorsally on the pygidium may be "pygidial eyespots". The distal end of the pygidium is yellow. Fading of pigmentation occurs to varying degrees with preservation.

Distribution

From Maine, Damariscotta River, Sheepscot River, and Orland River; and from Canada, Kennebecasis River, Saint John Estuary, and Minas Basin, Nova Scotia (personal communication from Dr. M. J. Dadswell on Canadian distribution).

Remarks

Criteria used by Fauchald (1968, 1977) to separate the four genera of Nephtyidae can be applied to determine the proper genus for this new species. The presence of interramal cirri prevents describing this animal as *Micronephthys*, which lacks these organs. Despite this animal's very small size when adult, with care, the slight but definite involution of the interramal cirri can be seen. This condition, and the presence of recurved, acicula tips, negate choosing Nephtys which has recurved interamal cirri and straight acicula tips. Two pairs of antennae, ornamentation of the proboscis, and the lack of eversible digitiform, nucal processes prevent considering this species as *Ineromonephtys* and justify placing it in *Aglaophamus*.

Ecology and behavior of adults

Aglaophamus neotenus lives in a polyhaline environment. Salinities at Wentworth Point in the Damariscotta River seldom drop below 30‰, those in the Orland River, and Montsweag Bay in the Sheepscot River, may decrease to about 19‰ in spring. Temperatures at all three locations are typical for Maine waters. All reach 0° C or less during the winter months, and as high as 17° C in late summer. Sediments associated with *A. neotenus* are mixtures of fine silt, clay, and sand grains, and include a large amount of organic material. The Orland River is unusual in that its sediment is composed of a very high percentage of wood chips. All three sites in Maine are sheltered from the open sea but exposed to tidal currents.

Adults from Wentworth Point and Montsweag Bay have a small ciliate associated with them. It appears to be of the order Peritricha and can be seen gliding over the inner surfaces of the parapodial rami. Hyman (1940) states that peritrichs can be epizotic and possibly ectoparasitic. The peritrichs on *A. neotenus* may be utilizing as food, particulate matter carried by the interramal currents. These ciliates do not appear to harm *A. neotenus* and the relationship may be commensal in favor of the ciliate.

In an attempt to determine the type of food eaten by *A. neotenus,* starved individuals were placed in dishes containing fresh *Mytilus edulis* tissue, dried liver powder, clumps of the brown diatom, *Phaeodactylum tricornutum,* and a green filamentous alga from the sediment surface at Wentworth Point, all materials which had been useful foods for other polychaetes in our laboratory. There was no response to these food materials.

The diet of *A. neotenus* was revealed when freshly collected specimens were observed voiding fecal pellets. The fusiform shaped pellets were encased in mucus, and connected to other pellets by a fine mucus string. Single pellets with a mucus string at one end were also observed. Pellets contained a mixture of materials including several species of benthic diatoms, empty copepod exoskeletons, unidentified organic material, and fine sand grains.

Aglaophamus neotenus moves in the usual manner of other nephtyids, burrowing actively and swimming when disturbed. Animals kept in an aquarium containing sediment were observed making burrows which opened to the surface. Movement in the sediment was active, and some swimming occurred when undisturbed. On occasion, worms were seen swimming 10 cm above the sediment.

Reproduction

Gravid females are easily distinguished by their pink or orange color and the presence of eggs densely packed in the coelom. The pink or orange color diminishes during the spawning period and the worms become whiter in color. Eggs extend into the parapodial rami, and are even observed in the coelomic space of an everted proboscis. In maturing females, eggs are fewer in number and only visible from setiger eight through the last setiger. Size of eggs in the coelom varies with maturity of the worm. The largest eggs measured inside preserved and cleared (glycerin mount) specimens, or histologically sectioned and stained females, were about 60 to 70 μm in diameter.

Spawning males are creamy white or yellow in color. Their coelomic spaces, including the parapodial rami, are slightly swollen with a fine, granular appearing material.

The Wentworth Point population had about twice as many males as females. Females were slightly larger than males. Further study is needed on sex ratios in this and other populations of *A. neotenus*. Preliminary histological studies showed a pre-spawning cytology for gravid adults to be similar to that of *Nephtys hombergii* and *N. caeca* as described by Olive (1978), but more detailed work must be done to determine precise differences or similarities.

Males and females were observed to spawn as they swam across the bottom of a culture dish. Males emitted a jet of milky fluid from the anus. The fluid took the form of a fine thread which, in a matter of seconds, dispersed into a milky cloud of sperm mixed with what appeared to be coelomic fluid. Eggs were released from females in a similar manner. Eggs moved down the coelomic cavity to the pygidial area and emerged from the anus in a fine string. The fluid accompanying eggs was more viscous than that with the sperm, and tended to remain visible with eggs as they settled to the bottom of the dish. In both sexes gametes were observed passing into the anal tract through a break in the coelomic wall. Individual worms known to have spawned, still contained gametes for over a month after initial spawning was observed.

Although adults from Wentworth Point contain gametes through the year, they are most obviously gravid in late winter and early spring. Spawning occurs in late March, April, and possibly early May (based on conditions of adults and the presence of planktonic stages in surrounding waters). Worms spawned "naturally" in the laboratory through April and May under the same temperature and salinity conditions found at that time off Wentworth Point.

Embryology

Eggs when released in the laboratory, are 45 to 80 μm in widest diameter and average 70 μm. They resemble flattened discs, much like human erythrocytes. Each egg contains a large granular nucleus with an accompanying nucleolus. The cytoplasm is granular, opaque, and white in color. Upon contact with sea water, eggs become spherical within 15 min and often show membrane invagination and clear bubble-like swellings at their surfaces.

Sperm are of the primitive metazoan type described by Franzen (1956). The head and mid-piece are 5 μm and the tail is 70 μm long. The tail ends in a fine hair-like tip. The spherical head contains a darkly staining nucleus, and there are four, round mitochondrial spheres in the mid-piece. A small, nipple-like acrosome is carried on the distal end of the head.

A detailed study of cleavage and cell-lineage was not done, but the general pattern of cleavage was observed, and appears typical of other annelids (see E. B. Wilson, 1892, and Kume and Dan, 1968).

A fertilization membrane appears 1 hr after fertilization. In five hours, a two-cell stage with distinct polar bodies is observed. The four-cell stage is reached in 6 hr, the eight-cell stage an hour later. During the following 10 to 15 hr, 16- and 32-cell stages are seen.

Larval development

Names of larval stages are after Gravely (1909).

Protrochophore. Twenty-four hours after fertilization a dense, dark green embryo (reflected light) is present inside the fertilization membrane. The anterior end is somewhat conical, and is composed of large embryonic cells. A prototrochal band of fine, short, beating cilia surrounds the equator of the embryo. Rotation inside the fertilization membrane does not occur. During the next 24 hr the prototroch protrudes through the fertilization membrane, and the larva begins to swim. This stage is 90 μm in widest diameter.

Early trochophore. An early swimming trochophore is seen in about 48 hr (Fig. 3A). The fine cilia of the protrochophore have been replaced with a single, well developed band of long cilia. This prototroch divides the larvae into two hemispheres, the anterior one being smaller. An apical tuft of long cilia protrudes at the anterior end of the larva. A gut is not present but the center of the early trochophore is packed with dense material, darker than the greenish-brown cytoplasm of the surface cells, when seen by reflected light. Small, yellowish-green pigment vacuoles and granules are scattered over the surface of the larva. The early trochophore is 90- to 100-μm long.

Trochophore. During the next 7 days, the early trochophore develops into a more advanced trochophore form (Fig. 3B). The fertilization membrane is adsorbed and becomes part of the larval cuticle. The surface of the cuticle is scattered with yellowish-green pigment vacuoles and granules, as in the early trochophore. The apical tuft is lost, but fine sensory cilia are distributed over the head. The prototroch has developed two rows of cilia, an anterior band of long cilia and a posterior band of fine, short cilia. (Only two rows of cilia could be seen clearly, but a third may be present.) Occasionally, a long, heavy cilium is observed laterally on the prototroch. Early in the trochophore stage no distinct gut is visible but during the next 4 weeks the dense material at the center of the trochophore develops into a ciliated cavity filled with yellowish-green, yolky material. A ciliated mouth opens during this period slightly posterior to the prototroch. A fine band of cilia, the neurotroch, extends from the mouth to the posterior surface of the trochophore. On several occasions, what appeared to be an anal opening was seen, but its presence was not confirmed. Precisely when in development the anus opens was not determined, but it is present in the Metatrochophore I stage. The trochophore is about 100 μm long.

The above descriptions represent larval development through about 30 days to the trochophore stage. It was not possible to raise trochophores to the Meta-

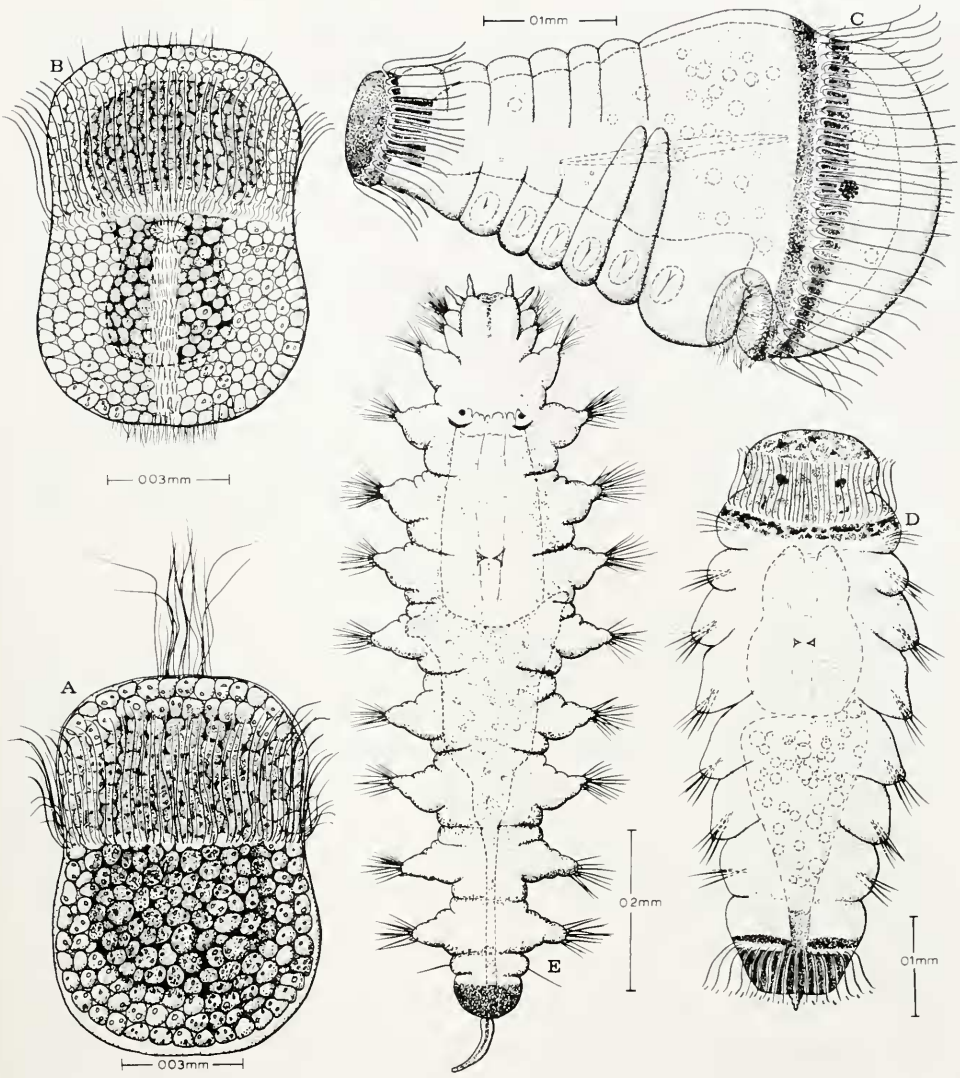

FIGURE 3. Larvae of *Aglaophamus neotenus*, new species: A, early trochophore; B, trochophore; C, Metatrochophore I with diatom present in gut; D, Metatrochophore II, E, juvenile.

trochophore I stage in the laboratory; however, Metatrochphore I and II stages were both collected from plankton tows and from sediment containing adult worms at Wentworth Point. These planktonic stages survived in the laboratory, and metamorphosed into juveniles whose characteristics were so like the adults as to dispel any doubt that they were young specimens of *Aglaophamus neotenus*.

Metatrochophore I. The simplest form of segment larvae, the first metatrochphore (Fig. 3C), appears in the plankton in May. When viewed laterally, the larvae are triangular in shape. Eyes are seen for the first time, a pair are lateral on the head, and slightly anterior to the prototroch. They are simple, round spots of red pigment granules. The prototroch is denser, but essentially the same as in the trochophore. A teleotroch has developed as a single band of long cilia

around the pygidium. The neurotroch is no longer present. A ciliated anus now opens on the posterior end of the larvae. Fine sensory hairs are still scattered over the head. The mouth has enlarged and a pair of ciliated lips has appeared. Up to six segments have formed, and setal sacs are present ventrally; dorsal sacs develop slightly later. Reflected light shows dark, reddish-brown pigment on both sides of the prototroch and telotroch. The distal portion of the pygidium is also heavily pigmented with the same reddish-brown pigment. Yellow pigment is found with the reddish-brown pigment. A complete gut is present, and it contains brilliant, yellowish-green, yolky material. The anal end of the gut, when viewed by reflected light, is filled with opaque, white yolky material. On several occasions diatoms were seen inside the gut. The Metatrochophore I is about 450 μm long. Specimens of this stage were raised into juveniles in the laboratory.

Metatrochophore II. In late May and early June the second metatrochophore stage, Metatrochophore II, is found in the plankton. It is cylindrical, with distinct prostomial and pygidial areas separated by segmental grooves from the setigerous segments (Fig. 3D). Parapodia are now present, and carry barred and smooth capillary tipped setate on both neuropodia and notopodia. Acicula have developed, and rest in small acicular sacs on the tips of the parapodial rami. Eyes are present dorsally on the prostomium, and have clear lenses posterior to comma-shaped spots of red pigment. The prototroch, having lost a band of cilia, and the telotroch, remain as single bands of long cilia. No other ciliation is seen except around the ventral mouth and the anus. A muscular pharynx with a pair of brown jaws is present, but the proboscis has not formed. The gut tapers from pharynx to anus. It is still colored a bright greenish-yellow, but contains fewer yolky vacuoles. The opaque, white yolky material is still present at the anal end of the gut. A small anal cirrus is seen ventral to the anus. Dark, reddish-brown pigment still surrounds the prototroch, but is less dense and has more yellow pigment associated with it. The head is covered with large, irregular-shaped spots of yellowish-brown pigment interspersed with dark red pigment granules. The telotrochal, and pygidial areas are still darkly pigmented, but have more yellow pigment associated with them than in the Metatrochophore I. The Metatrochophore II stage grows from six to eight setigers during its planktonic life and is about 550 μm long.

Metamorphosis. In June the eight-setiger Metatrochophore II undergoes a brief swim-crawl stage, sheds its larval ciliation, and burrows into the sediment. This is the beginning of metamorphosis. Approximately two weeks later, most of the larval characteristics are lost and a ten-setiger juvenile has developed.

Juvenile. The ten-setiger juvenile is about 800 μm long, it is essentially a minature adult (Fig. 3E). The body shape view dorsally is adult like, and gross morphology of the prostomium and pygidium resembles that of the adult, with antennae and an anal cirrus well developed. Eyes like the adults are present on setiger three. They may represent migration of prostomial eyes of the earlier Metatrochophore II posteriorly, as described by Fewkes (1883). Juvenile parapodia are well formed and carry ciliated, interramal cirri with accessory cirri. Ventral neuropodial cirri are present on all setigers. All adult setal types are seen in well developed fascicles, acicular sacs carry brown acicula. The retracted proboscis with a pair of triangular jaws can be seen through the translucent body wall and occupies setigers three through five. Dark pigment spots, pygidial eyespots are present on the pygidium. Pigmentation is otherwise transitional between the Metatrochophore II and mature adult.

Larval behavior

No larval stage showed either positive or negative phototaxis in the laboratory. Locomotion was observed. The protrochophore is a feeble swimmer, but in the early trochophore, and trochophore stages, active swimming occurs with the larva spiraling around its longitudinal axis as it moves through the water. The Metatrochophore I is a strong swimmer, but spiraling was not observed in this stage. The Metatrochophore II is much slower in its swimming than previous stages, and often drops to the bottom to "test" the sediment in a swim-crawl like manner. Juveniles move actively through the sediment, and make mucus-lined burrows. The head of a juvenile often protrudes slightly from a burrow. Juveniles were not observed to swim above the sediment.

Feeding seems to occur fist in the Metatrochophore I, as diatoms were observed in the digestive tract of this stage (Fig. 3C). No evidence of actual digestion was seen except the presence of oil-like vacuoles in the digestive tracts of Metatrochophore I and II stages, which appeared to be from digested diatoms. The digestive tracts of juveniles were filled with a brown organic material, and they may be feeding on sediment, as do the adults.

Discussion

Aglaophamus neotenus is an unusual member of its genus. The adult has a confusing mixture of what are normally considered larval and adult characters, as pointed out in a personal communication from Dr. Kristian Fauchald of the Allan Hancock Foundation. Larval characters are strong ciliation of the branchiae and the presence of pygidial eyes. Adult characters include the well developed proboscis and parapodial lobes. *Aglaophamus neotenus* appears to be the only member of its genus that reproduces at such a small size.

The retention of some larval characters as an adult, and the attainment of sexual maturity at a small size justify referring to *A. neotenus* as a neotenic species.

The fact that fecal pellets of *A. neotenus* contain several types of diatoms, the remains of copepods, and other sediment materials indicates it is a nonselective omnivore and feeds by ingesting sediment. This support Sanders (1958, 1960) who examined the gut contents of *Nephtys incisa* and concluded that it was a deposit feeder. Clark (1962) felt nephtyids were carnivores, and Mare (1952) found the remains of other polychaetes in the gut of a specimen of *Nephtys* sp. It now appears that there is a range from omnivore to carnivore in the Nephtyidae, with some feeding selectively and others nonselectively.

Comparing the development of *A. neotenus* with information given by previous workers reveals the general aspects of development in Nephtyidae. The early stages described by D. P. Wilson (1936) for *N. hombergii* closely parallel those of *A. neotenus*. Ciliation is the same in the trochophores of both species except that Wilson observed two small patches of cilia anterior to the prototroch and three rather than two bands in the prototroch. Pigmentation is generally the same in both species and part of the cuticle is formed by absorption of the fertilization membrane in both cases. The apical tuft is lost in *N. hombergii* at about the same time as in *A. neotenus*. Wilson observed a distinct anus in *N. hombergii* trochophores; this structure was unclear in *A. neotenus*. *Nephtys hombergii* has eggs which are 32 μ larger than *A. neotenus;* the trochophore in *N. hombergii* is 60 μ larger.

Fewkes (1883) describes a stage of *Nephtys* sp. which is significant, because

it is transitional between the trochophore and Metatrochophore I stage. This stage was no longer spheroidal but had elongated to double the original hemispherical length. Little growth had occurred in the preoral lobe, rather, most elongation had taken place in the postoral area. Green coloration had appeared around the pole of the preoral lobe. Most of the cilia (early trochophore cilia) which were scattered over the external surface of the body had disappeared. The lower body hemisphere was described as becoming elongated and segmented but no definite parapodial structures had developed in the several body segments. The intestine had lengthened and its walls and those of the stomach were still green as in younger larvae. Fewkes illustrated this stage which showed a well developed prototroch and telotroch.

Metatrochophore I stages have been observed for the Nephtyidae by several authors: Fewkes (1883) and Haecker (1896)—*Nephtys* spp.; Leschke (1903) and Thorson (1946)—*Nephtys ciliata.* The Metatrochophore I of *A. neotenus* agrees with those described by these workers. Common to all are: a triangular shape when viewed laterally; ciliation restricted to a prototroch and a telotroch; dorsal eyes anterior to the prototroch; a distinct green, yolky gut, sometimes containing diatoms; and dark reddish-brown pigmentation on the pygidial area and at the bases of the telotroch and prototroch. The Metatrochophore I attributed to *N. ciliata* by Thorson is larger than that stage in *A. neotenus* by about 100 μ.

Metatrochophore II stages were described by the following authors: Claparède and Metschnikow (1869), Fewkes (1883), Gravely (1908), and McIntosh (1908) —*Nephtys* spp.; Hofker (1920), and Thorson (1956)—*N. caeca;* Smidt (1944) and Thorson (1946)—*N. ciliata;* and Thorson (1946)—*N. hombergii.* The general features in various descriptions given for the Metatrochophore II agree with my findings for *A. neotenus:* a body form which is more or less cylindrical with distinct prostomial and pygidial areas; dark red eyes present dorsally on the prostomium; well developed parapodial lobes carrying setal fascicles; preacicular barred setae; ciliation restricted to a telotroch and prototroch; a pharynx with jaws but lacking a proboscis; a dark green, yolky gut narrowing to an anus; an anal cirrus developing on the ventral surface of the pygidium; and dark pigment covering the pygidium and present to a lesser degree around the prototroch. Metatrochophore II stages attributed to the genus *Nephtys* are about 100 μ longer than this stage in *A. neotenus.*

There is not enough specific information given in the literature to make a key which would separate the various nephtyid stages described from larvae of *A. neotenus,* but possibly pigment patterns could be used to separate nephytid larvae. Fewkes (1883) used color patterns of the anal area to identify larvae of different stages of the same species of *Nephtys* sp. obtained from the plankton.

There is no previous report of swim-crawl or settling activities of nephytids in the literature, and juvenile stages have not been described.

Metamorphosis from the Metatrochophore II into juveniles has not been reported, although Fewkes (1883) discussed the migration of eyes from the prostomium to setiger four in Metatrochophore II stages of *Nephtys* sp. He felt that migration was caused by the forward growth of the head and anterior body segments.

Attempts to rear nephtyid larvae in the laboratory fail after about 30 days. Fuchs (1911), working with *N. hombergii,* raised larvae to the trochophore stage in about 14 days, after which no further development took place. All died within 30 days. The same was true for D. P. Wilson (1936) with *N. hombergii* and in

my work with *Aglaophamus* sp. I do not think food is a limiting factor. The trochophores are densely packed with yolky material and a planktotrophic existence is unlikely in early stages. The presence of minute amounts of contaminants such as formalin, detergents and other organics are known to limit and even stop larval growth in many invertebrates. This may have been one factor which limited my success. Other factors such as the density of larvae in culture, light, temperature, and proper agitation may influence success or failure. As in any culture procedure, duplication of the natural environment is difficult and success may depend on the tolerance of a species to conditions imposed on it in the laboratory.

In this study Metatrochophore I stages were collected from the plankton and then reared to juveniles whose characteristics were so like the adults as to dispel any doubt that they were the same species. Metatrochophore II stages were also found in the sediment associated with the adult population, and also grew into juvenile specimens of *N. neotenus* in the laboratory. The challenge still remains to maintain nephtyid trochophore stages beyond 30 days, and raise them to Metatrochophore I stages which will then grow into juveniles and adults in the laboratory. This study nevertheless presents the most complete life history to date of any species in the family Nephtyidae.

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Summary

1. Populations of a previously undescribed polychaete, *Aglaophamus neotenus*, were found in three polyhaline locations on the Maine coast. Specimens were also received from Canadian workers. Temperatures in the Maine locations ranged from 0° C in winter to 17° C in the summer.

2. Diagnostic characters of the adult include heavily ciliated, involute interramal cirri which bear accessory cirri, present from setiger 5, sometimes 6, through setigers 15 to 20; the presence of acicula with recurved tips, capillary tipped, barred and spinous setae, and the lack of furcate setae; two pairs of antennae on the prostomium; ornamentation of the proboscis; the lack of eversible digitiform nucal processes; and the presence of pygidial eyespots on a spherical pygidium which is ringed with red pigment.

3. Adults reproduced at a size smaller than was previously reported in the Nephtyidae. Spawning was observed in the laboratory. Sperm are primitive. The eggs are granular, white in color, and resemble human erythrocytes in shape. Eggs average 70 μ in widest diameter.

4. Cleavage was spiral and appeared similar to that of other polychaetes.

5. Larval stages included: protrochophore, early trochophore, trochophore, Metatrochophore I, Metatrochophore II, and an eight-setiger swim-crawl-stage. Metamorphosis of the swim-crawl stage resulted in a ten-setiger juvenile which was essentially adult in morphology.

6. Behavior of adults and larvae was observed. Adults burrowed actively

and swarm above the sediment even when undisturbed. Larvae swam vigorously in early stages but slowed down as the swim-crawl stage was approached. Juveniles burrowed actively through the sediment and made mucus-lined burrows.

7. The diet of *A. neotenus* was studied. Larvae are lecithotrophic through the trochophore stage but diatoms were observed in the gut of Metatrochophore I stages. Observation of gut contents indicated juveniles feed on sediment. The digestive tract of adults contained materials, revealed by the contents of fecal pellets, which demonstrated that they were nonselective omnivores, feeding on sediment.

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